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MORPHOLOGY, FLAVONOID CHEMISTRY, AND CHROMOSOME NUMBER OF THE CHENOPODIUM NEOMEXICANUM COMPLEX

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The genus *Chenopodium* is generally recognized as very difficult taxonomically. Often it is almost impossible to circumscribe species with certainty because no sharp morphological discontinuities appear to exist in particular groups or complexes of plants. This paper represents the first of a series that will be devoted to the systematics of western North American species of *Chenopodium*. The investigations will utilize flavonoid chemistry, field studies of natural populations, micromorphology, chromosome numbers, and morphology.

This report is concerned with the results of a study of a group of triangular-leaved, attached-pericarp chenopods that are restricted to Arizona, New Mexico, Texas, and northern Mexico, here referred to as the *Chenopodium neomexicanum* complex. They occur typically in disturbed, weedy roadside habitats in mountains above 1650 m elevation. Individuals apparently are not common; collections in herbaria are few, and I have had some difficulty in locating plants in the field.

Chenopodium neomexicanum was described by Standley (1916) in

his treatment of Chenopodiaceae for the North American Flora. In the same publication, he proposed three additional species, namely, *C. palmeri, C. arizonicum,* and *C. parryi.* Standley distinguished these four taxa on the basis of such characters as seed size, length of leaf blades, shape of leaf apices (rounded vs. acute), odor of the plants, and whether the plants were upright vs. spreading from the base.

Aellen (1929) described *Chenopodium lenticulare,* a species closely related to the taxa previously erected by Standley. Aellen concluded that *C. parryi* was synonymous with *C. arizonicum,* and he also made *C. palmeri* the basis of the new subspecies *eu-berlandieri* of the species *C. berlandieri.* Why Aellen did not take up the name *palmeri* for this new taxon is not clear. Aellen alluded to *C. neomexicanum* as being a member of this complex of species, but he neither recognized it formally nor placed it in synonymy. He simply placed a question mark after the name, which I take as an indication that he was unsure of its proper placement.

The treatment of this group by Aellen and Just (1943) was the same as that of Aellen (1929) except they placed *C. neomexicanum* under *C. watsonii* forma *glabrescens.* Apparently Aellen had decided on this placement shortly after his 1929 manuscript had gone to press. The type specimen bears his annotation (1929), indicating that he chose to recognize the taxon at the varietal level instead of as a forma. This combination was never published.

Wahl (1952–53) recognized *C. palmeri* as a species and treated *C. arizonicum* as a synonym of it. He thus did not accept the ideas of Aellen (1929) and Aellen and Just (1943) that *C. palmeri* belongs with *C. berlandieri.* I consider this to be a very fundamental difference in interpretation. Wahl treated *C. neomexicanum* as distinct from *C. watsonii* f. *glabrescens,* and he placed *C. lenticulare* under the former. Wahl's concept of species in *Chenopodium* is clearly different from those of previous workers. He makes no mention of *C. parryi.*

Reed (1969) agreed with Wahl that *C. neomexicanum* and *C. lenticulare* are synonymous. He does not concur with Wahl's recognition of *C. palmeri* as a distinct species. Instead, he agrees with Aellen (1929) and Aellen and Just (1943) in placing the species under *C. berlandieri.* Reed also considers *C. arizonicum* to be the same as *C. palmeri,* and thus likewise puts it with *C. berlandieri.* In essence, then, he agrees with Wahl that both *C. palmeri* and *C. arizonicum* are the same, but he feels that they are not distinct from *C. berlandieri.*

Clearly, workers have held and continue to hold widely divergent views on the taxonomy of these chenopods. The purpose of the present study was to answer the following questions: (1) How many species should be recognized within the so-called *Chenopodium neomexicanum* complex? (2) Are any or all of the taxa in the *C. neomexicanum* complex distinct from *C. belandieri*? (3) What are the relationships of the *C. neomexicanum* complex within the genus?

Materials and Methods

Field collections and observations were made during the late summers of 1971 and 1972. When available, at least five plants were collected from each population.

Fruits were measured to the nearest 0.05 mm utilizing a dissecting microscope with an ocular micrometer. Ten determinations were made for each plant, and the mean was taken as the value for the individual.

For the epidermal studies, leaves were cleared in 5% sodium hypochlorite followed by 25% chloral hydrate. They were then dehydrated in an ethyl alcohol-xylene series, and mounted in balsam.

For the chromosomal studies, root tips from germinating seeds were pretreated with 0.2% aqueous colchicine for four hours before fixation in ethyl alcohol: acetic acid (3:1 v/v). The fixative was washed out with several changes of 70% ethyl alcohol. Chromosomes in the dividing cells were stained using the alcoholic hydrochloric acid-carmine technique as described by Snow (1963).

Flavonoid compounds were extracted from the plants by eluting them in absolute methanol for 24 to 48 hours. All parts of the plants contained the same flavonoids, and thus whole plants were used. The compounds were separated by two dimensional chromatography using 46 x 57 cm sheets of Whatman 3 MM paper. The procedures employed for the determination of chromatographic profiles and the identification of individual compounds are standard ones (Mabry, Markham, and Thomas, 1970; Crawford, 1973). In all instances at least two plants from each population sample collected by the author were analyzed chemically to check for intrapopulational variation. When sufficient material was not available for paper chromatography (collections other than those of the author), flavonoid profiles were determined on thin layer plates coated to a thickness of 500 μ with avicel-ph-101 microcrystalline cellulose.

All specimens, except the types, which are in US, are deposited in RM.

Results

Morphology. Standley (1916) employed leaf blade length as a taxonomic character, and used it for distinguishing between *C. palmeri* and *C. arizonicum*. My studies indicate that this feature is rather constant and similar in these plants, if comparable leaves are considered. The most important factor influencing size of the blades on a particular plant is the degree of maturity of the individual. The first leaves to develop along the central stem (the primary ones) are larger than any that appear later. These leaves are also the first to fall from the plant. Secondary leaves develop on side branches that come from the axils of primary leaves. Reduced bractlike leaves are produced on the upper part of a plant, both directly below and as a part of the inflorescence. The important point is that there are no consistent differences in leaf size between plants, if comparable leaves are considered. Plants fall into two groups on the basis of leaf blade length (fig. 1). It is of interest to note, however, that

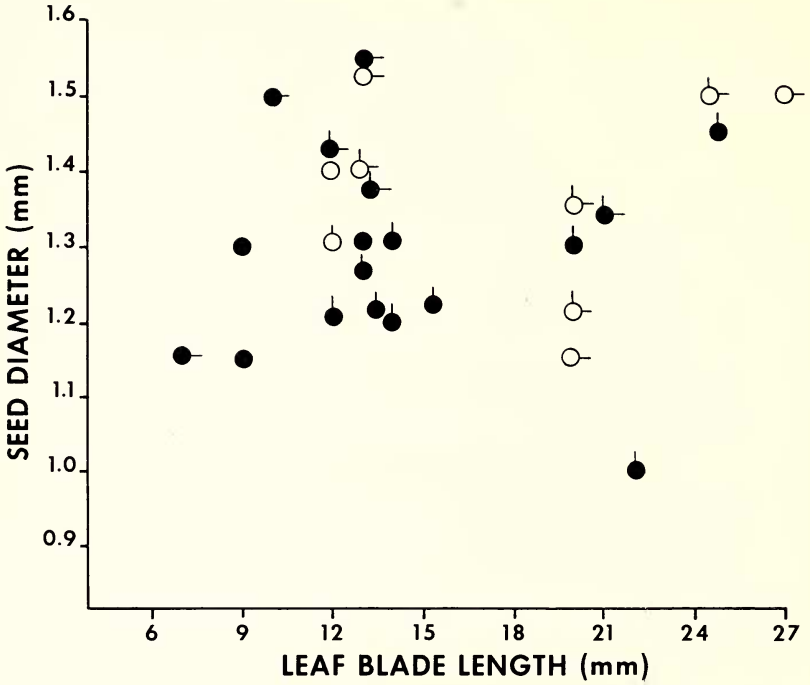

FIG. 1. Pictorialized scatter diagram depicting characters of individual plants in the *C. neomexicanum* group. Open circles represent plants that are basically upright, whereas closed circles indicate basally-branching individuals. Horizontal arms depict plants with leafy inflorescences, and the absence of arms indicates leafless or nearly leafless inflorescenses. Vertical arms show plants with bipartite basal lobes on the leaves, the absence of such arms represents plants with leaves having entire basal lobes.

those individuals with the smaller leaves are quite mature and bear only secondary leaves. By contrast, the plants with the larger leaves are less mature and still have the primary ones present.

Standley (1916) considered the nature of the leaf apex (rounded vs. acute) to be of taxonomic significance. Current investigations show that this feature, like leaf size, depends to a large degree on whether a leaf is a primary, a secondary, or a reduced upper one. A rounded apex is characteristic of most primary ones, whereas acute apices occur on secondary and bractlike leaves. This can be demonstrated by studying plants in which all types of leaves are present (fig. 2).

The presence or absence of bipartite basal lobes on leaves has been used as a diagnostic character in this group (Wahl, 1952–53). My data indicate that this feature is quite variable and is not correlated with other characters (fig. 1). Field investigations show it to be variable at the intrapopulational level.

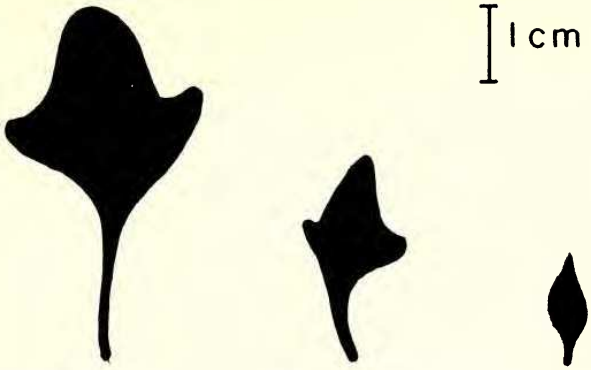

FIG. 2. Silhouettes of primary, secondary, and upper reduced leaves from an individual plant of *C. neomexicanum*.

The leaves of all plants within the *C. neomexicanum* complex are similar in that they are basically triangular in shape with lobes at or near the base. The margins above the basal lobes are invariably entire (fig. 3A,B). By contrast, the leaves of *C. berlandieri*, while somewhat variable in shape, are not basically triangular, and they have no pronounced basal lobes. In addition, the margins are variously toothed above the base (fig. 3C—E). Although these differences are not striking, they are consistent.

Two other morphological characters that have been used in the *C. neomexicanum* group are whether the plants are basically upright vs. spreading from the base with well developed branches and the degree of leafiness of the inflorescences. I have found it impossible to apply either feature with any degree of consistency. Neither character is correlated with other morphological features (fig. 1), and both are variable within individual populations. Also, it is of interest to note that the type sheet of *C. lenticulare* contains one plant that is strongly upright, whereas the other individual is freely branched from the base.

Standley (1916) considered *C. parryi* to be the only foul-smelling species of this complex. Aellen (1929) indicated that all taxa have a bad odor. Current studies of fresh and crushed dried material show that none is fetid. The only taxa that are truly malodorous are *C. watsonii* and *C. glabrescens,* both of which will be treated in a later paper.

Fruit size and shape are usually consistent features within species of *Chenopodium*, and many authors have used them as a basis for separation of species within this complex. Present investigations indicate that this is not feasible within the *C. neomexicanum* group. The fruits vary from 1.0 to 1.55 mm in diameter, and there are no gaps nor discontinuities in the variation pattern (fig. 1). In addition, no other characters are consistently associated with plants that have fruits of a particular size. Measurements of fruits from different plants from several populations have revealed that fruits may vary from 1.10 to 1.40 mm in diameter

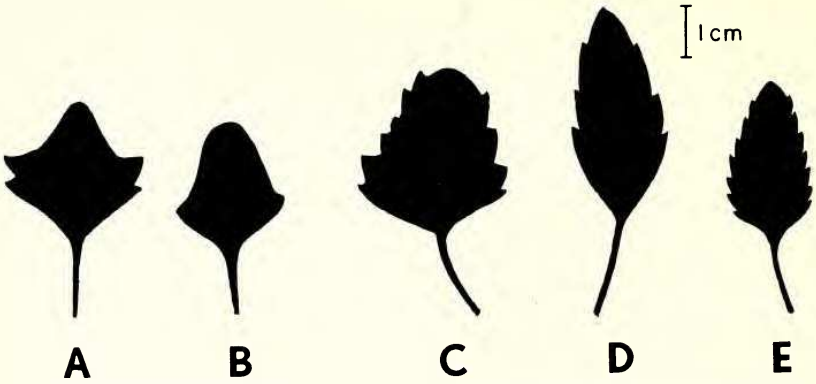

FIG. 3. Silhouettes of primary leaves of *Chenopodium*. A–B of *C. neomexicanum;* C–E of *C. berlandieri.*

within a population. Whether the margin is obtuse or rounded vs. acute is likewise extremely variable at the intrapopulational level and is impossible to apply as a taxonomic character.

Fruits of *C. berlandieri* have a conspicuous yellow area (appearing light in color) at the base of the persistent styles whereas those of the *C. neomexicanum* complex never display this feature (fig. 4). This character of *C. berlandieri* fruits was mentioned by Wahl (1952–53), and I have found it to be reliable for separating this species from the *C. neomexicanum* complex.

In members of the *C. neomexicanum* group the sepals are strongly spreading at maturity and wholly expose the fruits. By contrast, the sepals of plants of *C. berlandieri* are never strongly spreading and do not expose the fruit to a very large degree (fig. 4).

Leaf Epidermis. The lower leaf epidermis was examined from plants from six populations belonging to the *C. neomexicanum* group. Three leaves from two different individuals of each population were observed. The epidermal cells have straight walls, and the guard cells range in size from 15 to 25 μ (fig. 5A). This range of sizes was found on individual leaves, and was not associated with different leaves on the same plant, different plants from the same population, nor plants from different populations. The mean length for all guard cells measured (over 200) was 21 μ.

An examination of the lower leaf epidermis from ten plants of *C. berlandieri* has shown that the pattern is similar to that found in the other group, but the epidermal and guard cells are consistently larger (fig. 5B). The range in guard cell length is 25 to 35 μ with the mean from the 100 cells examined being 30 μ.

Chromosome Numbers. Chromosome numbers were determined from germinating seeds from three different populations (Arizona, Apache

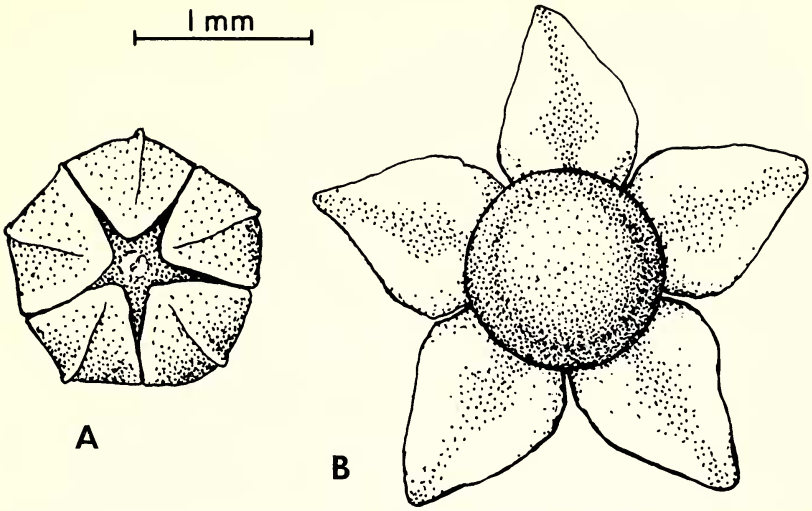

FIG. 4. Fruits and sepals of *Chenopodium*. A, *C. berlandieri* with enclosing sepals and light (actually yellow) area around the style base on the fruit; B. *C. neomexicanum* with spreading sepals that expose the fruit.

Co., ca 5 mi W of Springerville, *Crawford 522;* New Mexico, Grant Co., 12 mi S of Silver City, *Crawford 722;* 9 mi S of Silver City, *Crawford 727*). All determinations proved to be **2n = 18,** and these agree with the one previous report (Keener, 1970) (Arizona, Pima Co., *Wahl 21826.*) Whereas little chromosomal information has been available for the *C. neomexicanum* group, there are several reports for *C. berlandieri* (Bassett and Crompton, 1971; Homsher, 1963; Keener, 1970; Mulligan, 1961); all tetraploid **2n = 36.**

Flavonoid Chemistry. Thirty individuals belonging to the *C. neomexicanum* group were examined for flavonoid constituents. The profiles for all of these plants are extremely uniform and are quite simple. All show two 3–*O*–glycosides of the flavonol quercetin; one is the rutinoside and the other is a rhamnodiglucoside. It should be emphasized that extracts from the type specimens of all species in this group yielded profiles on thin layer plates that appeared identical to each other. In addition, these patterns corresponded to those obtained on paper in which extracts from my own collections were used.

The flavonoid constituents of *C. berlandieri* differ from those of the *C. neomexicanum* complex. The two share quercetin 3–*O*–rutinoside, but differ in other components. Spectral studies show that both produce only quercetin but the R_f values of the compounds demonstrate that, except for the rutinoside, the sugars attached to the quercetin nucleus differ in the two. Over ten collections of *C. berlandieri* were studied chemically, and the difference between the profile of this species and that of the other group is consistent.

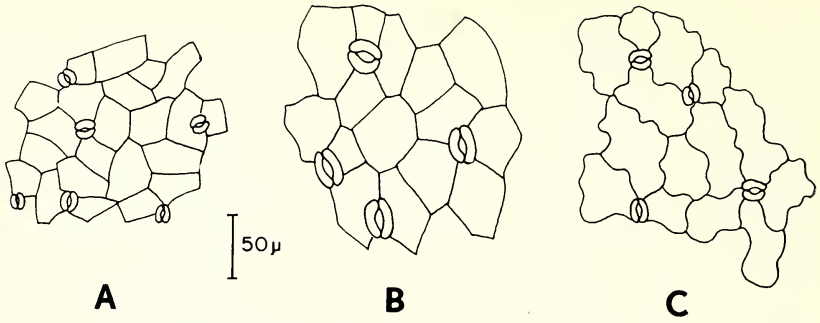

FIG. 5. Camera lucida drawings of the lower leaf epidermis of *Chenopodium*. A, *C. neomexicanum*; B, *C. belandieri*; C, *C. fremontii*.

DISCUSSION AND CONCLUSIONS

The present study has demonstrated that morphological features that have been employed for distinguishing the five "species" in the *C. neomexicanum* group are not consistent. Additionally, the combinations of characters that have been alleged to circumscribe taxa indeed do not occur (fig. 1). Previous workers, particularly Standley (1916), picked individual plants that exhibited certain features as the types for species. The distinctive characters of these plants are the result primarily of their maturity and do not reflect genetic differences. For example, the holotype of *C. arizonicum* is an extremely mature plant with all primary leaves missing and only secondary and bract-like ones remaining. By contrast, the type specimen of *C. palmeri* is a much less mature individual with primary leaves intact. It is obvious that the "key" characters used by Standley to separate the two taxa, i.e., leaf length and apex shape, reflect this difference in maturity.

Collections and field studies have shown that features such as seed size and shape, leafiness of inflorescence, presence or absence of bipartite basal lobes on the leaves, and upright vs. spreading plants are variable within populations. As a result, it is not possible to place most individuals into one of the previously recognized five species.

Plants belonging to this complex can be distinguished morphologically by the fact that they have triangular leaves with basal lobes, and seeds with attached pericarps that have reticulately roughened surfaces. Although this may not appear to be many characters on which to recognize a species, no other taxon in *Chenopodium* possesses these features. In this genus, where species are notoriously difficult to delimit morphologically, these plants are relatively well circumscribed.

Flavonoid chemistry is a unifying feature of the *C. neomexicanum* complex. That the type specimens of all described species appear to be the same chemically is of particular interest. Also, no intra- or interpopulational chemical variation was encountered in those plants examined.

These data assume greater importance when it is considered that this chromatographic profile, so far as is known, is unique in the genus.

The leaf epidermal pattern found in this complex also appears to be a unifying feature. Due to small sampling, I cannot say that similar patterns are not found in other taxa. It is of interest to note, however, that the pattern does differ strikingly from that found in *C. fremontii* (fig. 5C), even though I have found it impossible to distinguish leaves of the two on the basis of external morphology. Preliminary studies indicate that epidermal patterns will be useful taxonomically in North American *Chenopodium* (Crawford, 1972).

When all data are considered, it seems best to recognize the *C. neomexicanum* group as consisting of a single species, namely *C. neomexicanum*. Even after the five formerly recognized species have been "lumped", the resulting taxon is much more uniform and tightly circumscribed morphologically than many others in *Chenopodium*.

The information at hand demonstrates quite conclusively that *C. neomexicanum* is distinct from *C. berlandieri*. Features of the leaves (fig. 3) and fruits and sepals (fig. 4) serve to separate the two species morphologically in all instances. Chromosomally, *C. neomexicanum* is diploid, whereas *C. berlandieri* is tetraploid. The flavonoid chemistry of the two is likewise quite distinct. Leaf epidermal patterns also are diagnostic features for separating the two species (fig. 5A,B). Although the patterns are basically similar, the difference in guard cell size is consistent.

I shall comment only briefly on the placement by Aellen and Just (1943) of *C. neomexicanum* under *C. watsonii* forma *glabrescens* (now *C. glabrescens* (Aellen) Wahl). There appears to be no justification for such a transfer, and I am in complete agreement with Wahl (1952–53) that this should not have been done. *Chenopodium glabrescens* may be distinguished on the basis of its fruits, which have conspicuously whitened, attached pericarps. In addition, the sepals enclose the fruits tightly, even in the most mature condition. There are differences between *C. glabrescens* and *C. neomexicanum* in both leaf morphology and leaf flavonoid chemistry (Crawford, unpublished).

Various features of *C. neomexicanum* raise interesting questions concerning its relationships within *Chenopodium*. Morphologically, the plants have triangular leaves that are essentially identical to those of *C. fremontii*. The seeds of *C. fremontii,* however, differ markedly from those of *C. neomexicanum* in that the pericarp of the former is smooth and easily separable. The seeds of the latter taxon are similar to those of *C. berlandieri* although, as mentioned above, they can be distinguished. Past workers have debated whether the leaves or seeds should be given greater weight in considering relationships. Standley (1916) placed the *C. neomexicanum* complex together with *C. fremontii* in his "group" Fremontiana, the unifying feature being the triangular leaves. Aellen (1929) suggested that those plants with "honey combed-pitted" seeds (as found in *C. neomexicanum* and *C. berlandieri*) should be grouped

together, but he also believed that it was more a matter of personal preference whether one chooses to use leaves or seeds as the basic criterion for taxonomic arrangements.

Chenopodium neomexicanum appears to be more closely related to *C. berlandieri* than it is to *C. fremontii*. Gross leaf morphology is the only feature that *C. neomexicanum* and *C. fremontii* share. The two differ in leaf epidermal patterns (fig. 5A,C). In addition, the flavonoid chemistry of the taxa is quite different. *Chenopodium fremontii* produces a series of kaempferol and/or isorhamnetin glycosides in addition to several quercetin glycosides (Crawford, 1972, and unpublished). It has already been mentioned that the seeds of the two species are very different. It would appear that even though the similarities between the leaves of the two are quite striking and evident, it gives a rather misleading impression of overall genetic relationships.

Based on the totality of characters, *C. neomexicanum* appears to be rather closely related to *C. berlandieri*. Although the two clearly represent distinct species, the following basic similarities should be noted: 1) the seeds of both have attached, reticulate pericarps; 2) the flavonoid chemistry of the two is similar in that they produce only quercetin glycosides; and, 3) the leaf epidermal patterns, while distinct on the basis of cell size, are quite similar.

The fact that *C. neomexicanum* is diploid and *C. berlandieri* is tetraploid is of evolutionary interest. The former taxon is the most *berlandieri*-like diploid chenopod that I have encountered. This at least suggests the possibility that plants similar to *C. neomexicanum* may be ancestral to *C. berlandieri*. Wahl (1952–53) indicated that *C. berlandieri* may have originated in the southwestern United States with speciation occurring in arid or montane areas. This hypothesis for the locality of the origin of *C. berlandieri* is near the present distribution of *C. neomexicanum*.

Taxonomy

Chenopodium neomexicanum Standley, North Amer. Flora 21:19. 1916. Type: USA: New Mexico, Sierra Co.: along Mineral Creek, 2250 m, 26 Sep 1904, *O. B. Metcalfe 1413*. Holotype: US!

Chenopodium palmeri Standley, North Amer. Flora 21:19. 1916. Type: Mexico: Chihuahua: Hacienda San Miguel, 1885, *E. Palmer 9*. Holotype: US!

Chenopodium arizonicum Standley, North Amer. Flora 21:19. 1916. Type: USA: Arizona: Santa Rita Forest Reserve, 1903, *D. Griffiths 5982*. Holotype: US!

Chenopodium parryi Standley, North Amer. Flor 21:21. 1916. Type: Mexico: San Luis Potosi: region of Cd. San Luis Potosi, 1878. *C. C. Parry & E. Palmer 780*. Holotype: US!

Chenopodium lenticulare Aellen, Feddes Report. Spec. Nov. Regni Veg. 26:152. 1929. Type: USA: Texas: Austin, 1918, *M. S. Young 708*. Holotype: US!

A list of specimens examined is available from the author upon request.

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ECOLOGY OF THE SAGUARO (CARNEGIEA GIGANTEA): PHENOLOGY AND ESTABLISHMENT IN MARGINAL POPULATIONS

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The saguaro, *Carnegiea gigantea* (Engelm.) Britt. & Rose (Cactaceae), has been at the center of much scientific interest since Shreve (1910) reported its failure to reproduce in some localities. Additional observations that supported Shreve's conclusion (Gill, 1942; Gill and Lightle, 1946; Hastings, 1961; Alcorn and May, 1962; Niering et al., 1963; Alcorn, 1966) led to a number of studies aimed at defining the cause of the saguaro's decline (Shreve, 1911; Lightle et al., 1942; Alcorn and Kurtz, 1959; McGregor et al., 1962; Hastings and Turner, 1965;